

- VAN der WEERD, A. (1973): Rodentia from pleistocene fissure filling near Athens. Proceedings K. Ned. Akad. Wet. (Phis. Sci.) 76, 148–166.
- WATERBOLK, H. T. (1968): Food production on prehistoric Europe. Science 162, 1093–1102.
- ZIMMERMANN, K. (1949): Zur Kenntnis der mitteleuropäischen Hausmäuse. Zool. Jb. (Syst.) 78, 302–322.

Anschrift des Verfassers: Dr. HORST ENGELS, Departamento de Zoologia, Universidade de Coimbra, Portugal

Age determination and mortality of the nutria (*Myocastor coypus*) in Maryland, U.S.A.¹

By G. R. WILLNER, K. R. DIXON, and J. A. CHAPMAN

*Appalachian Environmental Laboratory, Center for Environmental and Estuarine Studies,
University of Maryland*

Receipt of Ms. 10. 6. 1982

Abstract

Male and female nutria were collected from the eastern shore of Maryland between 1974 and 1977. Data on body measurements from these animals were used to develop models to determine the ages of nutria. These age estimates then were used to construct a life table for the nutria population. The measurements utilized to age nutria included body lengths, body weights, tooth eruption, and hind foot lengths. The tooth eruption techniques permitted separation of nutria into distinct age classes. Eighty percent of the nutria were classified as two years old or younger.

Three models were compared to determine the age of nutria by body measurements. The model of best fit was $Y = (Y_{\max} - Y_0)(1 - e^{-bt}) + Y_0$ where Y_{\max} and Y_0 are the maximum and minimum values of the dependent variable respectively, and t is the age. Based on various validation analyses, this model accurately predicted age by body length and hind foot length. An age distribution for males and females measured and released in the field was calculated. Females collected in year 1975 were used to construct a mortality schedule. Eighty percent mortality occurred in the first year of life, declining slightly in age class 2 and 3.

Introduction

There has never been a definitive study on the population dynamics and age structure of nutria (*Myocastor coypus*) populations. The reason for this has been attributed to the lack of adequate techniques for the determination of age of nutria in the field. Two recent papers have shown that a relationship between body weight and age does exist (DIXON et al. 1979; WILLNER et al. 1980). The purpose of this study is to present data on age-specific body weights, hind foot lengths and body lengths of male and female nutria for the development of a model that can be used to predict age by body measurements, and to develop a life table for Maryland nutria.

¹ Contribution Number 1360 – AEL of the University of Maryland, Center for Environmental and Estuarine Studies, Appalachian Environmental Laboratory. Financial support for this study was provided in part by the Federal Aid to Wildlife Restoration Act for Maryland W-49-R. Computer support was provided by the University of Maryland Computer Science Center.

Age determination and growth

Several body measurement criteria have been used to determine the age of nutria. ALIEV (1965) described in detail the growth and development of ranch nutria from birth to six years of age. Included in the discussion is a description of molar eruption and wear that can be used to age nutria. BROWN (1975) determined the age of nutria by arbitrary body size and pelage characteristics. Juvenile pelage was wooly in appearance and the animals weighed less than 1.25 kg. Subadults weighed between 1 and 4.25 kg and the pelage was in the process of moulting. Adults weighed 4.0 to 8.0 kg, with females weighing a maximum of 7.5 kg. ADAMS (1956) classified animals with a hind foot length of 10.9 cm from heel to claw to be less than three months old (immatures); a 11.2–12.4 cm length to be three to five months old (subadult); and 12.7 cm length to be more than five months (adults).

Several methods of determining the pattern of body growth with respect to age are possible: 1. individual animals kept in captivity can be weighed and measured at successive time intervals; 2. animals can be marked as juveniles and recaptured several times throughout their lifespan and weighed and measured at each capture; 3. individual animals can be captured, weighed and aged at the same time. Advantages and disadvantages of each of these methods were outlined in WILLNER et al. (1980). These authors developed a method of determining body growth by capturing nutria twice and avoiding sacrificing the animal for age determination purposes. The predictive model used to determine the weight gain pattern of nutria was:

$$W = (W_{\max} - W_0)(1 - e^{-bt}) + W_0 \quad (1)$$

where W_{\max} is the maximum value of weight of a nutria, b is obtained from the regression and W_0 is the initial weight at birth, 227.36 g.

This model was compared with two other models of body measurements as a function of age; the model of best fit then was used to estimate the age of nutria collected in the field. The resulting age distribution was used to calculate a life table for the nutria population (see WILLNER [1982] for a detailed review of other aspects of nutria biology).

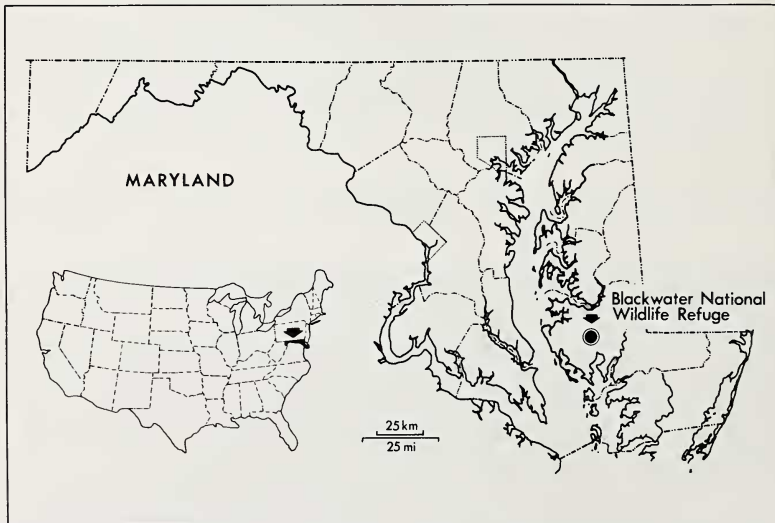


Fig. 1. Map showing the location of the Blackwater National Wildlife Refuge located in Dorchester County, on the eastern shore of Maryland U.S.A.

Study area

The study area is located on a brackish marsh at Blackwater National Wildlife Refuge and surrounding state-owned land at Fishing Bay in Dorchester County, Maryland (latitude 38°, 26', longitude 76°, 08', elevation 0 to 2 m) (Fig. 1). Situated within the coastal plain of Maryland, the refuge is composed of 70 % open water and marshland, 20 % wooded areas and 10 % of agricultural fields. The dominant tidal marsh plants present are the three square rush (*Scirpus olneyi*), salt reed grass (*Spartina cynosuroides*) and narrow leaf cattail (*Typha angustifolia*). Loblolly pine (*Pinus taeda*) grows in the sandy soil. Corn (*Zea mays*) and soybeans (*Glycine max*) are produced in alternate years. The refuge is divided into twelve management units that are leased to fur trappers during the commercial trapping season which runs from January to March, and occasionally includes the month of April. In addition to nutria, muskrat (*Ondatra zibethicus*), fox (*Vulpes vulpes*) and otter (*Lutra canadensis*) are trapped on the refuge.

Feral nutria have lived in the wetlands of the eastern shore of Maryland since the early 1940's. The population on the refuge reached nearly 4000 in 1975 before it was decimated by the 1976–77 winter. The mean temperature in January 1977 was below 0 °C for several days and the annual snowfall was double that of the previous two years. The history of the population has been documented by WILLNER et al. (1979).

The climate of the study area was generally humid, subcontinental with an average of 109 cm of annual precipitation including 38 cm of snowfall. Winters are usually mild and temperatures rarely go below -4.5 °C. Summer temperatures above 35 °C are not uncommon. Nonetheless, the nutria must be considered as being at their extreme northern range on the east coast of North America. This was demonstrated by the decimation of the population during the winter of 1976–77.

Methods and materials

Animal collection

Animals for this study were collected between the years 1974 and 1977. A total of 604 nutria carcasses were collected for necropsy. Nutria were weighed on an autopsy scale and body measurements were recorded. Attempts were made to collect nutria for each month of the year. During the trapping season, animals were obtained from trappers. In other months, animals were trapped with leg-hold traps, sacrificed and returned to the laboratory. In addition, a total of 544 animals were tagged, measured, and released in the field during the study period. One hundred and forty-nine of these 544 animals were trapped and returned to the laboratory where they were frozen and necropsied. The sample of 604 includes these tagged animals obtained from trappers.

Sex determination

Sex of adult nutria was determined by external genitalia (MAURICE 1931; EHRlich 1958). The female genitals consist of a vaginal orifice and a prominent papilla. The vaginal orifice is below but contiguous to the urinary papilla. The external genitalia of the male nutria consists of a penis, prepus, and a glans penis which contains an os baculum. The penis lies about 5 mm above the anal area.

Age determination

Age of nutria were determined by the tooth eruption and wear of molars as described by ALIEV (1965). All skulls were examined at the same time and placed in age categories from six months to six years. This procedure reduced the error caused by placing them in the wrong age category, particularly the older age groups (2 + years).

Skulls originally classified as six months were further divided by the length of the maxillary tooth row (LMR); skulls with LMR of less than 17 mm were placed in age category .25 years; LMR of 17 to 23 mm in age category .50 years; and LMR of greater than 23 mm in age category .75 years. Lengths of the maxillary tooth row were obtained by the number of molars present in young animals. By the time nutria have reached their first birthday, all four molars have erupted and examination of tooth wear is subjective. Old animals exhibit extreme wear, particularly around the first and second molar.

Field studies

Nutria were tagged and released during a population estimation study between 1974 and 1977 (WILLNER et al. 1979). Since the reward system for obtaining nutria "in-the-round" was not initiated until 1975, not all animals could be used for necropsy. Of the 247 recovered, 149 were acquired for laboratory study. For most animals handled in the field, body measurements, weights, location, method of capture, extent of injury, parasite load, and sex were recorded.

Statistical analysis

Data analysis

Data were analyzed using programs from the Statistical Package for Social Sciences (SPSS) and the Biomedical Package (BMD). Male and female data were analyzed separately.

Regression analysis

Nonlinear least square regression models were fitted to the data, with age as the independent variable. Three models were compared using body length, body weight and hind foot length as the dependent variables. In the nonlinear form, the models are:

- 1) $Y = (Y_{\max} - Y_0) (1 - e^{-bt}) + Y_0$
- 2) $Y = a 10^{b/(t+c)}$
- 3) $Y = a t^b$

where Y is the dependent variable (body length, weight, hind foot length)

t is the independent variable (age)

Y_{\max} is the theoretical maximum value that the dependent variable can obtain

Y_0 is the value of the dependent variable at birth

a , b and c are constants

Model number 1 is the model developed and used to obtain body weight gain patterns in DIXON et al. (1979) and WILLNER et al. (1980). Model number 2 is a modification of a model used by DUDZINSKI and MYKYTOWYCZ (1961). According to (GOSLING et al. 1980) the constant c should equal the gestation length of the animal. Length of the gestation for the nutria is 4.34 months. Higher values for r^2 , the coefficient of determination, were obtained in this study when the constant c was set at zero. Model number 3 was taken from SOKAL and ROHLF (1969). This model is known as the allometric growth curve and used to describe "organisms where the ratio between increments in structures of different size is relatively constant, producing a relatively great increase of one variable with respect to the other on a linear scale" (SOKAL and ROHLF 1969 : 478). These models describe the relationship between body measurements and age of nutria.

Comparison of non-linear models

The three non-linear models were compared by the chi-square analysis: (FREUND 1971)

$$F = \frac{\chi_1^2/DF}{\chi_2^2/DF}$$

If no significant difference was found between models, the model of best fit was determined by the lowest mean residual sum of squares found in the regression analysis.

Validation and verification

The model of best fit was validated on a separate set of data not used in the original analysis. Methods used to validate the model of best fit included graphical techniques as well as two statistical tests: the paired t-test and determining whether the slope in a regression of predicted or observed values is significantly different from 1.

The paired t-test used was presented by LAW (1979): where \bar{x}_i was the mean of the observation for each age class i for each body measurement and Y was the observation for the predictive set of the data. The test statistic used was:

$$\bar{d} (n) = \Sigma d_i / n \quad (2)$$

where d is the difference between the observed (\bar{x}) and predictive (Y) value, and n is the size of the sample. The variance was

$$S_d^2(n) = \sum (d_i - \bar{d}(n))^2 / (n - 1) \quad (3)$$

A confidence interval around d (n) was calculated as:

$$\bar{d}(n) \pm t(n - 1, 1 - \alpha/2) \cdot \sqrt{S_d^2(n)/n} \quad (4)$$

where t is the value from a t table. The model is considered validated when the confidence interval includes zero.

To determine if the slope of the regression was significantly different from 1.0, the test statistic used was (SOKAL and ROHLF 1969: 424):

$$t_s = (b - 1) / s_b \quad (5)$$

where

$$s_b = \sqrt{s_{Y \cdot X}^2 / \sum X^2}$$

Weighting of measurement variables

A weighted average of the variables used for age determination was obtained using the inverse of the residual mean squares obtained from the regression analysis as a weighting factor (SOKAL and ROHLF 1969: 178).

$$\bar{S}_t = \frac{\sum w_i S_t_i}{\sum w_i} \quad (6)$$

where, S_t , the variable, is weighted by the factor w (the inverse mean residual sum of squares). Weighting was done to place more emphasis on the measurement with the least variability in the data.

Age determination of field animals

Male and female nutria with hind foot measurements, body weights, and/or body lengths were aged with the model of best fit, using the parameters from the non-linear regression. The three calculated ages were then weighted as described above and an average value recorded for each nutria. These animals were then combined with animals aged by the tooth eruption method (ALIEV 1965) and used to determine mortality schedules.

Mortality schedule

Mortality rates of the Maryland nutria population were determined by constructing a life table based on age-specific death rates. A life table was produced based on the methods and assumptions as stated by CAUGHLEY (1977). The method takes into consideration that nutria produce at a birth flow rather than at a birth pulse (reproduction at a particular season) (CAUGHLEY 1977: 92).

... "the age distribution is calculated at the birth pulse for a population with a stable age distribution and known rate of increase. The frequency of the zero age class is calculated from the fecundity rates. Each age frequency is multiplied by e^{rx} and then divided by the number in the zero age class to give a table of l_x (the probability of surviving)." . . .

The rate of increase, r , can be calculated from population estimates for two years or more. The formula for this is from CAUGHLEY (1977: 109):

$$r = \frac{\sum N_t - (\sum N) (\sum t) / n}{\sum t^2 - (\sum t)^2 / n} \quad (7)$$

where N is the density estimate transformed to natural log; n is the number of estimates and t is the time units of one year. For this paper, " r " was calculated using population estimates for 1974 and 1975 from Unit B of Blackwater National Wildlife Refuge (WILLNER et al. 1979: 24, Table 8).

This method assumes that animals used in the study were taken from its summer and winter range; that the animals were not killed by a disaster (i.e. flood); that the age distribution is stable; that the sample is composed of at least 150 animals; and that no age class is selected for (or against) due to some behavior difference. The method also requires that the sample should be collected within a short time frame.

Little information is available for constructing life tables for birth flow populations. CAUGHLEY (1977) noted that the method for preparing a life table as stated above would be invalid if the "birth flow population with a zero rate of increase has a stable age distribution equivalent to an l_x schedule beginning from an age of half a year" (CAUGHLEY 1977). To adjust for the birth flow population the l_x schedule was computed by averaging l_x for two years (DEEVEY 1964)

$$L = \frac{l_x + l_{x+1}}{2}$$

A mortality schedule was constructed from females collected in 1975.

Results

Tooth eruption and wear

Based on tooth eruption and wear eight distinct age classes were apparent in Maryland (Table 1). This technique has been used by several investigators (SCHITOSKEY 1972; DIXON et al. 1979; WILLNER et al. 1979; WILLNER et al. 1980). Unfortunately the technique can be

Table 1

Age distribution of Maryland nutria as determined by tooth eruption and wear (ALIEV 1965)

Age (years)	Number	Percent
Fetus	2	0.45
0.5*	130	29.55
1	69	15.68
2	181	41.14
3	45	10.23
4	11	2.50
5	1	0.23
6	1	0.23
TOTAL	440	100.00

*includes animals of age class 0.25, 0.50 and 0.75

used only on animals which have been killed. Another problem with this method is that the skulls are often crushed by trappers, making them useless for aging purposes. Of the 604 nutria collected, 164 (27%) were not useable. The method of age determination described herein could be used with greater precision if known age animals are available.

Age determination by body measurements

The use of body measurements for age determination in mammals has been suggested for a wide array of taxa (SANDERSON 1961; HILL 1971). The purpose of this section is to develop a model using body weight, body length and hind foot length in

combination for estimating ages of nutria. Three different models were tested, keeping sexes separate.

Body measurements

Various body measurements of male and female nutria were recorded from animals collected for necropsy and from animals trapped and released in the field. Body weights of nutria were recorded in grams. Animals that were pelted were not weighed. Body lengths were measured from the tip of the nose to the base of the tail. Measurement of the tail was recorded but not considered as a suitable method for age determination since a number of animals had lost a major portion of their tail due to frostbite injury. The third measurement used was hind foot length taken from the tip of the claw to the heel. No animals with frostbite injury to the feet were included in the analysis, particularly those collected during the winter of 1976-77 (see WILLNER et al. 1979:29 Fig. 18).

Mean values of body measurements increase with age in both the male and female nutria (Figs. 2-4). A dramatic increase is obvious in animals less than one year of age. For males, the smallest hind foot measured was 59 mm; the largest was 156 mm. For females the smallest and largest foot measured was 70 mm and 142 mm, respectively. The range of the body lengths measured varied between 189 mm to 727 mm in males and 305 mm to 600 mm in females. Body weights of males ranged from 167 g to 8690 g; females weighed from 624 g to 7343 g. Hind foot lengths and body lengths of females less than 0.75 years of age had consistently higher mean values than the males with the same measurements. This

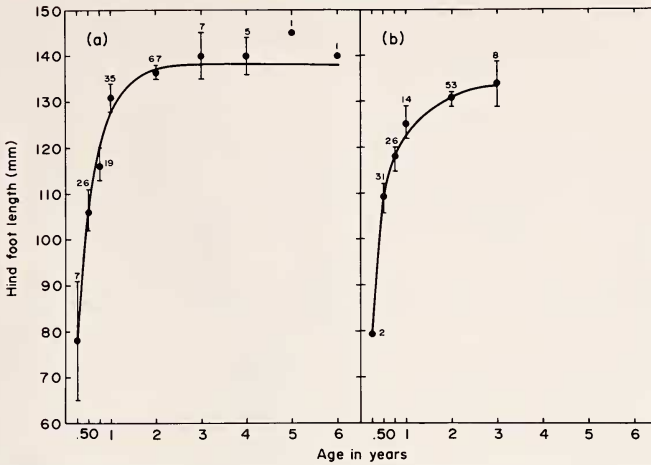


Fig. 2. Predicted and observed hind foot lengths by age of feral male and female nutria from Maryland. Error bars are 95 % confidence intervals. Sample sizes are shown. Predicted hind foot lengths are represented by curve. (a) males; (b) females

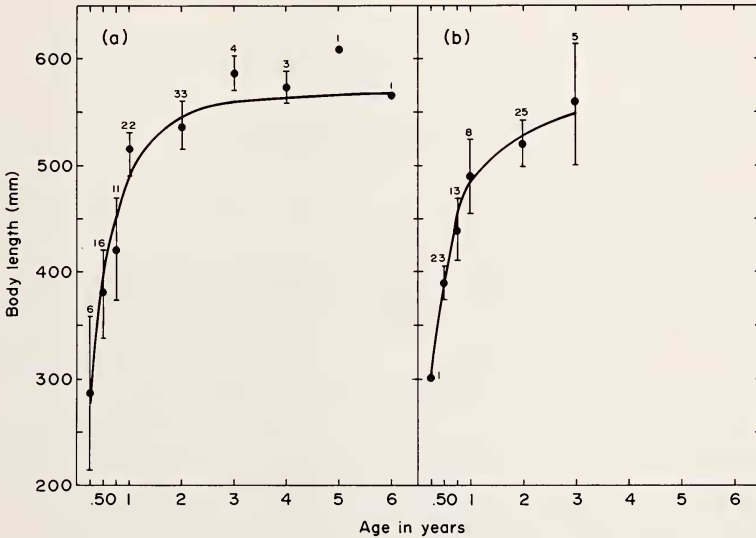


Fig. 3. Predicted and observed body lengths by age of feral male and female nutria from Maryland (a) males; (b) females

also occurred in female body weights for ages 0.50 and 0.75. However, the trend reversed for animals one year and older and males maintained consistently higher mean values than the females. Results of t-test analysis indicate no significant differences between the body measurements by sex and age until the animals are over one year of age.

Non-linear regressions

A total of nine non-linear least squares regressions were performed. The regression required that initial values of parameters be included for each model. These values were obtained from linear least squares regression analysis. Pair-wise comparisons of the models

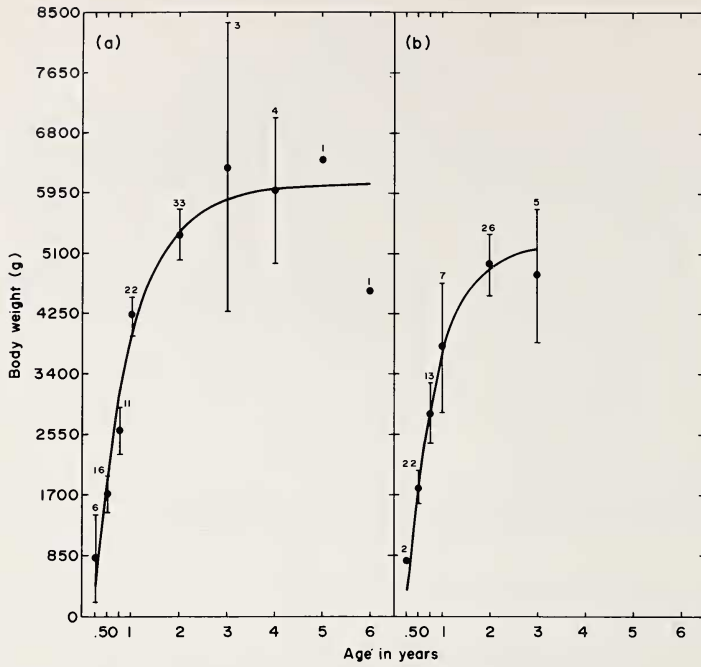


Fig. 4. Predicted and observed body weights by age of feral male and female nutria from Maryland (a) males; (b) females

Table 2

Comparison of the non-linear models by chi-square analysis (FREUND 1971)

	Hind Foot Length *F Value	Significance	Body Length F Value	Significance	Body Weight F Value	Significance
Male						
Model 1 vs. Model 2	1.15	NS	1.02	NS	1.02	NS
Model 1 vs. Model 3	1.75	P < 0.05	1.19	NS	3.14	P < 0.05
Model 2 vs. Model 3	1.51	P < 0.05	1.17	NS	3.08	P < 0.05
Female						
Model 1 vs. Model 2	1.13	NS	1.07	NS	1.03	NS
Model 1 vs. Model 3	1.31	NS	1.05	NS	1.30	NS
Model 2 vs. Model 3	1.17	NS	1.02	NS	1.26	NS
Model 1) $Y = (Y_{\max} - Y_o)(1 - e^{-bt}) + Y_o$						NS = not significant
Model 2) $Y = a10^{b/(t+c)}$						* $(F = \frac{\chi_1^2/DF}{\chi_1^2/DF}, \chi_1^2 > \chi_2^2$
Model 3) $Y = at^b$						

were made for both males and females on each independent variable by chi-square analysis (Table 2). In cases where there was no significant difference between models, the model of best fit was selected based on the lowest mean residual sum of squares as derived from the formula:

$$\text{MRSS} = (\text{residual sum of squares}) / (N - K)$$

where the sum of squares is (observed-predictive)², N is the number of animals in the sample and K is the number of parameters used in the non-linear model. Table 3 summarizes the values obtained from the mean residual sum of squares for each model for

Table 3

Mean residual sum of squares obtained from the non-linear regression for 3 models

	Model 1	Model 2	Model 3
Male			
Hind foot length	66.34	68.45	105.44
Body length	4300.30	4316.96	4975.94
Body weight	68691.40	706846.30	1148575.00
Female			
Hind foot length	45.86	44.62	55.87
Body length	2104.50	2091.95	2197.90
Body weight	760393.50	773509.40	921494.80

three measurements. To keep the method of aging field animals consistent, only one model was selected as the model of best fit. For males, model 1 had the lowest mean residual sum of squares (MRSS) for hind foot length, body length and body weight (Table 3). In females, however, this model had the lowest MRSS value only for body weight. The difference between that model and the other two was not significant, therefore for consistency, Model 1 was selected. The regression analysis produced predictive measurements for each age class (Figs. 2 to 4).

Validation and weighting of variables

One hundred and forty-nine cases (76 males, 73 females) not used in the original analysis were used for validating the model. Regression of predicted on observed values was forced through the origin. The predictive value and an observed value for every measurement in each age class was obtained. Plots of the actual observed measurements variable and the predicted measurement values are shown in Fig. 5 to 7. Body length and hind foot length measurements for males and females show a close fit.

Statistical validation tests were performed on the mean predicted measurement variable and the observed variable, using the paired t-test (LAW 1979), and the test for determining whether the slope is significantly different from one (SOKAL and ROHLF 1969). Table 4 summarized the results of those tests. In all cases except female body weight no significant differences were found ($P > 0.05$). Female body weight declines with age as seen in WILLNER et al. 1980: 345, Fig. 2. Each age class had a lower observed value than its predictive value for female body weight (Fig. 6). The model is considered validated for body length and hind foot length. Allowance for the variability in female body weight was made in age determination of field animals by the weighted averaging procedure. Variables were weighted by the inverse of the mean residual sum of squares (Table 3).

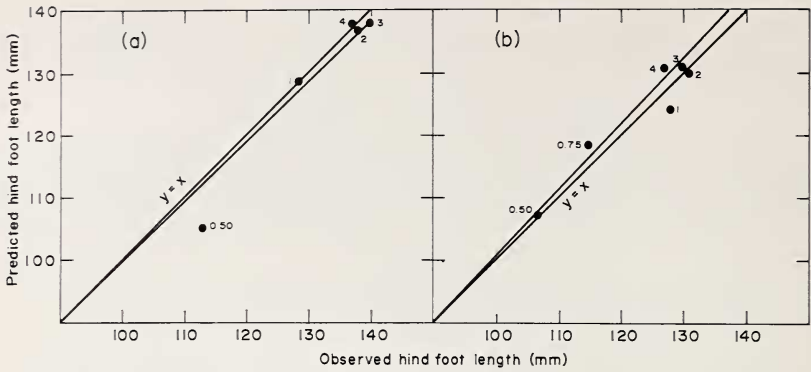


Fig. 5. Weighted regression of predicted hind foot lengths against observed hind foot lengths of feral male and female nutria from Maryland. Age class is given next to data points. Dots represent mean values from data set used to validate model, $(Y_{\max} - Y_0)(1 - e^{-bt}) + Y_0 = Y$, (a) males; (b) females

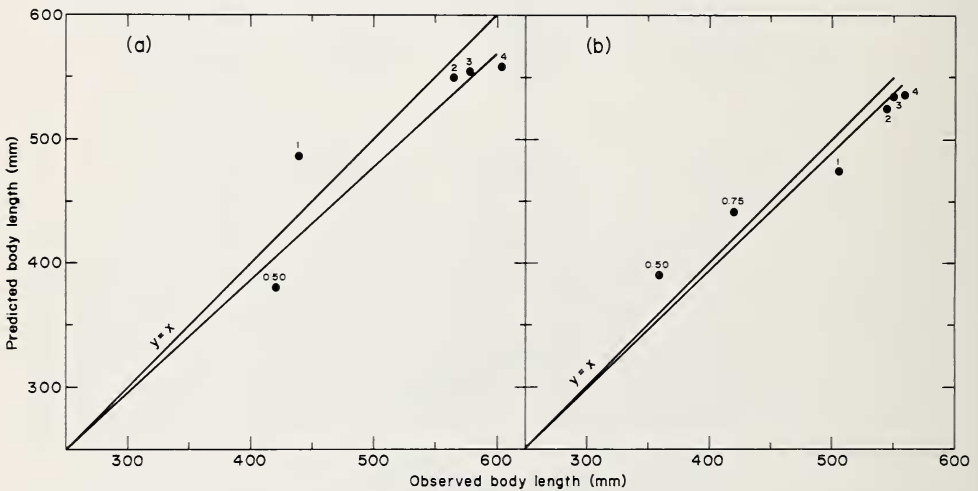


Fig. 6. Weighted regression of predicted body lengths against observed body lengths of feral male and female nutria from Maryland. Age class is given next to data points. Dots represent mean values, (a) males; (b) females

Age determination of field animals

A total of 544 nutria were measured in the field between 1974 and 1978. Only those animals captured between 1974 and 1976 were aged by the model of best fit. This was to avoid dealing with animals that survived the 1976–1977 winter. Distribution of the predicted ages for the field animals are presented in Tables 5 and 6. In all years (1974–1976) the age classes with the largest number of nutria are one year and younger with very few animals in the older age classes.

For purposes of obtaining a mortality schedule and life table, these animals were combined with those which were originally aged by tooth eruption and wear. Age distributions of female nutria with animals aged by the two methods are presented in Table 7. The largest age classes again are one year or younger. Forty percent of the population consisted of juveniles (less than one year old) (Table 7). Nutria greater than two years of age made up less than 12 percent of the overall age distribution.

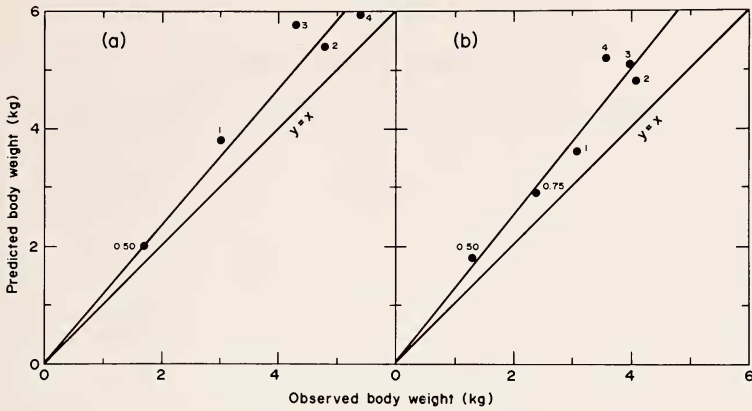


Fig. 7. Weighted regression of predicted body weights against observed body weights of feral male and female nutria from Maryland. Age class is given next to data points. Dots represent mean values (a) males; (b) females

Table 4

Results of validation tests performed on the model:

$$(Y_{\max} - Y_0) (1 - e^{-bt}) + Y_0 = Y$$

Variable	Paired T-test 95% confidence interval on T	Test of Regression Coefficient	
		t_b	Significance of t_b
Male			
Hind foot length	2.096 ± 4.39	-.99	P > 0.05
Body length	17.127 ± 45.613	.11	P > 0.05
Body weight	-672.73 ± 608.34	.23	P > 0.05
Female			
Hind foot length	-1.45 ± 2.11	1.33	P > 0.05
Body length	6.306 ± 23.996	1.05	P > 0.05
Body weight	823.88 ± 446.20	6.5	P < 0.05

Mortality

The format used to construct a mortality schedule for female nutria collected in year 1975 follows CAUGHLEY (1977:92-93 Table 8. 6).

Sampled frequency

To estimate the number of animals in the zero age class, it was necessary to determine the fecundity rate. This was accomplished by taking the number of young in a litter (WILLNER et al. 1979, Fig. 23) for each age class and adjusting for the number of females per litter. WILLNER et al. (1979) calculated that the overall sex ratio for fetuses favored females (80 males to 100 females) (56% females). Again adjustments were made to this figure to account for the number of females that are pregnant in a population as well as the number of embryos that are not resorbed. WILLNER et al. (1979) found that about 65 percent of the

Table 5

Predicted age distribution of male nutria

Field collections of nutria were made between 1974 and 1976. Age is determined by applying measurements to model $(Y_{\max} - Y_0)(1 - e^{-bt}) + Y_0 = Y$

Age	1974		1975		1976	
	Frequency	Percent	Frequency	Percent	Frequency	Percent
0.25	1	2.6	9	5.7	4	4.1
0.50	2	5.3	27	17.2	13	13.4
0.75	6	15.8	25	15.9	10	10.3
1	20	52.6	61	38.8	40	41.2
2	6	15.8	22	14.0	23	23.7
3	-	-	-	3.2	4	4.1
4	3	7.8	8	5.1	3	3.1

Table 6

Predicted age distribution of female nutria

Field collections of nutria were made between 1974 and 1976. Age was determined by applying body measurements to model $(Y_{\max} - Y_0)(1 - e^{-bt}) + Y_0 = Y$

Age	1974		1975		1976	
	Frequency	Percent	Frequency	Percent	Frequency	Percent
0.25	4	10.5	17	13.5	10	15.4
0.50	7	18.4	28	22.2	8	12.3
0.75	5	13.2	23	18.3	11	16.9
1	14	36.8	32	25.4	22	33.8
2	2	5.3	18	14.3	5	7.7
3	-	-	4	3.2	2	3.1
4	6	15.8	4	3.2	7	10.7

female population are pregnant in a given year with 9.8 percent of the embryos being resorbed. Animals six months old produce 1.38 litters per year; animals one year and older produce 2.76 litters per year after a gestation length of 4.34 months. The sum of all the age-specific fecundity rates, 470.08 (Table 8) was used as an initial calculation for the sample frequency in the mortality schedule (Table 9).

Corrected frequency

The corrected frequency was determined by multiplying the sampled frequency, f_x by the correction factor, e^{rx} . The value "r", the intrinsic rate of increase, was determined by the density estimates at Blackwater National Wildlife Refuge in Cambridge, Maryland using eq. 7. The calculated value of r equaled the value of 0.22, indicating an increasing population for years 1974-1975.

Table 7

Age distribution of female nutria

Age determination by tooth eruption or by model $(Y_{\max} - Y_0)(1 - e^{-bt}) + Y_0 = Y$

Age	1974		1975		1976	
	Frequency	Percent	Frequency	Percent	Frequency	Percent
0.25	5	8.9	18	9.5	10	8.8
0.50	13	23.2	40	21.2	23	20.4
0.75	7	12.5	40	21.2	16	14.2
1	15	26.8	34	16.9	33	29.2
2	9	16.1	45	23.8	22	19.5
3	1	1.8	8	4.2	2	1.8
4	6	10.7	4	2.1	7	6.2

Table 8

Calculation of fecundity rates of female nutria for mortality schedule of age class zero

Age	Number of young in litter	Number females in litter per female per year*	Frequency of females	Age-specific fecundity rate
**0.50	4	1.77	80	141.6
1	3.8	3.37	34	114.58
2	3.9	3.46	45	155.7
3	5.5	4.85	8	38.8
4	5.5	5.85	4	
				470.08

*Adjusted for

1. 80m:100 f or 55.55% of litter consisted of female nutria.
2. 35.1% of females not pregnant (64.9% pregnant).
3. 9.8% of litter resorbed (90.2% not resorbed).
4. 1.38 litters per year for age class 6 months; 2.76 litters per year for age class 1 to 3.
5. i.e. $(4)(.649)(.902)(.555)(1.38) = 1.77$

**Combines age class 0.50 and 0.75.

Smoothed frequency

The smoothed frequency was determined by applying a logpolynomial regression (CAUGHLEY 1977:96)

$$\text{Log}_{10}(f_x) = a + bx + cx^2 + dx^3$$

where a was the y intercept, x was the independent variable, age and b, c, d were constant values obtained from the regression.

Table 9
Mortality schedule for female nutria collected in year 1975

Age x	Sampled frequency f_x	Correction factor e^{rx} ($r = 0.22$)	Corrected frequency $f_x e^{rx}$	Smoothed frequency F_x	Life Table			
					l_x	L_x	d_x	q_x
0	470.08	1.00	470.08	419.99	1.0000			
1	34.00	1.25	42.37	66.29	.1578	.578		.794
2	45.00	1.56	69.87	34.19	.0814	.119	.459	.589
3	8.00	1.93	15.48	7.78	.0185	.049	.070	.633
4	4.00	2.41	9.64	7.1	.0169	.031	.018	.031

Life table

Using the above information, a life table for female nutria collected in year 1975 was determined (Table 9). The l_x schedule referred to as survivorship, is the probability at birth of an individual surviving to age x . The oldest female nutria obtained was four years of age. The d_x schedule, mortality, is the number of deaths that occur during age interval x to $x + 1$. The q_x schedule was the mortality rate which is the number of animals that die during age x . To adjust for birth flow, the L_x schedule was determined by averaging two survivorship schedules together (DEEVEY 1964 :32). Survivorship, mortality and mortality rates were calculated for one year intervals only, omitting age classes 0.25 to 0.75. The high mortality rate of nutria as juveniles is consistent with other r -selected species which reach sexual maturity early, have more than one large litter per year, and have a short life span (DIXON and SWIFT 1981). During the first year of life the mortality rate is nearly 80 percent, declining only slightly in the succeeding years to about 60 percent in age class 1-2 and 63 percent in age class 2-3 (Table 9).

Discussion and conclusions

A model was developed for predicting the age of nutria by body measurements using data from animals that were aged by the tooth eruption and wear technique. Using hind foot lengths, body lengths, and body weights, the model predicts age for both males and females. Three models were compared, selecting the best fit model by statistical analysis. Mortality schedules were then determined from these age distributions.

The basis of the model is the calculation of age for each nutria using body measurements. Predicted ages were determined using data from nutria that were aged by standard techniques (ALIEV 1965). The method of age determination by body measurements can be applied to other species as well. The validation of the model can be improved by using animals with known ages. The information obtained can be used to calculate age specific information such as turnover rates and mortality schedules.

Visual scans and statistical analyses were performed to validate the model. The predicted results from independent data sets were found not statistically significant from the observed ($p < 0.05$) for body and hind foot lengths. Significant differences were found between predicted and observed values of body weights of females. The model for body weights of males was validated by one of the two tests used. This can be explained by the variability that exists within the body weight data that were used. The point that must be considered is that the model's accuracy is dependent on the reliability of the original

method of estimating the age classes. It was assumed that the age determination technique for ranch nutria applies to feral nutria, although no studies have been conducted to confirm this.

The development of a statistical method for age determination by body measurements can have wide application to a number of other species where it is not possible to age by standard age techniques such as by weight of eye lens, bone ossification, cementum annuli of teeth all of which require sacrificing animals. Once age distributions are determined, the information can be used to determine age-specific fecundity rates, life tables, stability of age distributions for several years, and in management practices that require optimizing for a specific age class.

Acknowledgements

The authors are grateful to KENT B. FULLER, DAN M. HARMAN, THOMAS F. REDICK and JAY R. STAUFFER, Jr., for reviewing the manuscript. MABEL LANCASTER and KATHRYN TWIGG typed the manuscript and DEBRA MCNABB prepared the figures. KARL DOERK prepared the German summary.

Zusammenfassung

Altersbestimmung und Sterblichkeit der Biberratte (Myocastor coypus) in Maryland, U.S.A.

Von 1974 bis 1977 konnten männliche und weibliche Biberratten in Maryland gesammelt werden. Daten von Körpermaßen dieser Tiere dienten der Entwicklung eines Modells zur Altersbestimmung. Diese Altersschätzungen wurden dann zur Ermittlung der Altersstruktur in der Population herangezogen. Folgende körperlichen Merkmale wurden benutzt: Körperlänge, Körpergewicht, Zahndurchbruch und Hinterfußlänge. Insbesondere die Ergebnisse an der Bezahnung erlaubten eine Zuordnung zu verschiedenen Altersklassen. 80 % der Nutria konnten als 2 Jahre alt oder jünger klassifiziert werden.

Zur Altersbestimmung mit Hilfe von Körpermaßen wurden 3 Modelle verglichen. Das beste wird durch folgende Formel beschrieben: $y = (y_{\max} - y_0)(1 - e^{-bt}) + y_0$ (y_{\max} und y_{\min} = Max. und Min. der abhängigen Variablen, b = Steigung, t = Alter). Dieses Modell ermöglichte am genauesten eine Altersbestimmung, wenn Körperlänge und Hinterfußlänge eingesetzt wurden.

Eine Anzahl 1975 gesammelter weiblicher Nutria wurde zur Bestimmung der Mortalitätsrate verwandt. Es ergaben sich 80 % Mortalität im 1. Lebensjahr mit leichtem Rückgang in den Altersklassen 2 und 3. Die durchschnittliche Lebenserwartung der Biberratte in Maryland liegt bei 2,5 Jahren.

References

- ADAMS, W. H., Jr. (1956): The nutria in coastal Louisiana. Proc. Louisiana Acad. Sci. 19, 28-41.
- ALIEV, F. F. (1965): Growth and development of nutrias' functional features. Fur Trade J. Canada 42, 2-3; 43, 2-3.
- BROWN, L. N. (1975): Ecological relationships and breeding biology of the nutria (*Myocastor coypus*) in the Tampa, Florida area. J. Mammalogy 56, 928-930.
- CAUGHLEY, G. (1977): Analysis of vertebrate populations. New York: John Wiley and Sons.
- DEEVEY, E. S., Jr. (1964): Life tables for natural populations of animals. In: Readings in Population and Community Ecology. Ed. by W. E. Hazen. Philadelphia: W. B. Saunders. pp. 32-63.
- DIXON, K. R.; SWIFT, M. C. (1981): The optimal harvesting concept in furbearer managements. In: Worldwide Furbearer Conference Proceedings. Ed. by J. A. CHAPMAN and D. PURSLEY. Maryland: Worldwide Furbearer Conf., Vol. II, 1524-1551.
- DIXON; WILLNER, G. R.; CHAPMAN, J. A.; LANE, W. C.; PURSLEY, D. (1979): Effects of trapping and weather on body weights of feral nutria in Maryland. J. Appl. Ecol. 16, 69-76.
- DUDZINSKI; M. L.; MYKYTOWYCZ, R. (1961): The eyelens as an indicator of age in the wild rabbit in Australia. CSIRO Wildl. Res. 6, 150-159.
- EHRlich, S. (1958): The biology of the nutria. Bamidgeh Bull. Fish Cult. Isreal 10, 36-43; 60-70.
- FREUND, J. E. (1971): Mathematical statistics. (2nd ed.) New Jersey: Prentice-Hall.
- GOSLING, L. M.; HUSON, L. W.; ADDISON, G. C. (1980): Age estimation of coypus (*Myocastor coypus*) from eye lens weights. J. Appl. Ecology. 17, 641-647.
- HILL, E. P. III. (1971): An evaluation of several body measurements for determining age in live juvenile cottontails. Proc. Ann. Conf. Southeastern Assoc. Game and Fish Comm. 25, 269-281.
- LAW, A. (1979): Simulation modeling and analysis. Unpublished notes. University of Wisconsin, Madison, Wisconsin.
- MAURICE, J. A. (1931): Le Ragondin. Arch Hist. Nat. Soc. Acclim., Paris, France.

- SANDERSON, G. C. (1961): Techniques for determining age of raccoons. Biological Notes No. 45. Nat. Hist. Survey Div.
- SCHITOSKEY, F., Jr. (1972): Bacular variation in nutria from southern Louisiana. Southwestern Naturalist 16, 431-459.
- SOKAL, R. R.; ROHLF, F. J. (1969): Biometry: the principles and practice of statistics in biological research. San Francisco: W. H. Freeman and Company.
- WILLNER, G. R. (1982): Nutria. In: Wild Mammals of North America: Biology, Management and Economics. Ed. by J. A. CHAPMAN and G. A. FELDHAMER. Baltimore and London: The Johns Hopkins Univ. Press.
- WILLNER; CHAPMAN, J. A.; PURSLEY, D. (1979): Reproduction, physiological responses, food habits and abundance of nutria on Maryland marshes. Wildlife Monograph 65, 1-43.
- WILLNER; DIXON, K. R.; CHAPMAN, J. A.; STAUFFER, J. R., Jr. (1980): A model for predicting age-specific body weights of nutria without age determination. J. Appl. Ecology 7, 343-347.

Authors' address: GALE R. WILLNER, KENNETH R. DIXON and JOSEPH A. CHAPMAN, Appalachian Environmental Laboratory, University of Maryland, Center for Environmental and Estuarine Studies, Frostburg State College Campus, Frostburg, Maryland 21532, U.S.A.

On the biology of the Egyptian Mongoose, *Herpestes ichneumon*, in Israel

By RINA BEN-YAACOV and Y. YOM-TOV

Zoology Department, Tel Aviv University, Israel

Receipt of Ms. 15. 7. 1982

Abstract

The biology of the Egyptian Mongoose was studied in Israel both in the field and in captivity. Daily and annual activity patterns are described, including social behaviour, reproductive biology, ontogenetic development and food habits.

Introduction

The Egyptian mongoose is one of the most common mammalian predators in Israel. It inhabits most of the country, except for desert habitats, but is more common in plains and valleys than in hilly areas. The mongoose prefers the vicinity of water or irrigated places and needs a certain amount of dense plant cover. As it is common near human settlements and has crepuscular habits it is relatively easy to observe, but in spite of these factors, surprisingly little is known so far about the biology of this species.

The present work is an attempt to study the biology and behaviour of the Egyptian mongoose in the field. Some complementary data were gathered from captive specimens reared in the Tel Aviv University Wildlife Research Centre (WRC) and from the Tel Aviv University Zoological Museum (ZM).